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Inter- and intraspecific variations of the chemical properties of high-Arctic mosses along water-regime gradients

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Abstract

We examined and compared the contents of organic chemical components (lignin-like compounds, total carbohydrates and extractives), carbon and nutrients (nitrogen, phosphorus, potassium, calcium, magnesium) among the mosses *Calliergon giganteum*, *Hylocomium splendens*, *Racomitrium lanuginosum*, and among three populations of *H. splendens* collected from habitats in contrasting water regimes in the Canadian high-arctic tundra. C:N:P ratios were analyzed among and within moss species. Mosses from hydric habitats had lower total carbohydrate and higher nutrients contents than did mosses from drier habitats; however, we found no intraspecific variations in nitrogen and calcium contents in the different populations of *H. splendens* along water-regime gradients. The contents in lignin-like compounds, extractives and carbon showed no clear trends along water-regime gradients. Mosses from hydric habitats had lower C:N, C:P and N:P ratios than mosses from drier habitats, although we found no intraspecific variations in C:N ratios in *H. splendens* along water-regime gradients. These results suggest that chemical properties of mosses, especially nutrient contents, are strongly correlated with water availability in high-Arctic tundra.

Keywords: Moss; Chemical property; Water availability; Intraspecific variation; High Arctic

1. Introduction

Bryophytes represent an important component of high-latitude ecosystems, where global warming is expected to have a pronounced effect on water availability (Robinson et al., 2003; Wasley et al., 2006). It is important to examine the effect of water availability on the ecophysiological traits of mosses in order to predict the impact of climate change on high-latitude vegetation. In this regard, the chemical properties of mosses have been documented as an indicator of ecophysiological traits of mosses. Güsewell (2004) and Britton and Fisher (2007) suggest nutrient stoichiometry is a useful indicator for assessing nutrient limitations or growth strategies in moss ecology. Many previous studies have examined interspecific variations in the chemical contents of Arctic and/or Antarctic mosses along gradients in water regimes (e.g. Christie, 1987; Davey, 1999; Parkarinen and Vitt, 1974; Vitt and Parkarinen, 1977).

Few studies have investigated variations within species, although such an approach can help us to

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interpret the effects of local environmental conditions on ecophysiological traits (Ueno et al., 2006). Intraspecific comparisons enable us to assess the acclimation of mosses to different water availability and nutrient conditions without consideration of phylogenic (or phylogenetic) differences. In addition, organic components and various nutrients in mosses are generally determined separately. The combined analysis of organic components and nutrients provides many materials with which consider the effect of water availability on chemical properties. To examine this problem, we compared the contents of organic components (lignin-like compound, total carbohydrates and extractives), carbon and major nutrients (nitrogen, phosphorous, potassium, calcium, and magnesium) among and within moss species collected in habitats of contrasting water regimes in the Canadian high-Arctic tundra.

2. Materials and methods

2.1. Study site

The study site was located on a glacier foreland, near Oobloyah Bay in the northern part of Ellesmere Island, Nunavut, Canada (80°51′N, 82°51′W). Microtopographic glaciation at this site has led to the development of patchwork microhabitats, each with its own water regime and dominant moss species. In brief, *Calliergon giganteum* grew predominantly in the mire which forms a part of a brook recharged mainly by permafrost runoff (hydric site); *Hylocomium splendens* ranged the vegetation from the edge of the mire (hydric site) to the top of the moraine (xeric site), and dominated the intermediate plain (mesic site) between both sites; and *Racomitrium lanuginosum* dominated the vegetation at the top of the moraine (xeric site).

2.2. Sampling

We collected the green shoot assemblages of the three dominant moss species described above, as well as those of three populations of *H. splendens* that grew under three different water regimes (hydric, mesic and xeric). The shoot assemblages in hydric site were tall and slender forms, while those in xeric site were compact and dense forms, and those in mesic site were intermediate forms. Six samples of each species/population were collected, except for *R. lanuginosum*, for which only four samples were taken. The samples were air-dried *in situ* and stored in sealed, cylindrical (60×30 mm), plastic containers before being transported to the laboratory for analysis. All moss samples were collected during 17–26 July, 2003 – the period of peak growing season at the study site.

2.3. Chemical analysis

The shoot assemblages were oven-dried at 80 °C for 48 h and then ground in a mill to yield particles <0.5-mm in diameter. Lignin-like compounds and extractive contents were obtained from the sample by sulfuric acid hydrolysis and alcohol–benzene extraction, respectively (King and Heath, 1967). The total carbohydrate content was measured using a phenol-sulfuric acid method (see Dubois et al., 1956). The total carbon and nitrogen contents were measured by automatic gas chromatography (NC analyzer SUMIGRAPH NC-900, Sumitomo Chemical, Osaka, Japan). After acid wet oxidation of each sample in $HNO_3 + HClO$, an ascorbic acid method was used to measure the phosphorus content (Olsen and Sommers, 1982). Flame photometry was used to detect the potassium content, and the calcium and magnesium contents were determined by atomic absorption. Details of these methods can be found in Osono and Takeda (2004a,b, 2005).

3. Results

We found clear interspecific variations in all the analyzed nutrients along the water-regime gradients (Table 1). Moss species from hydric sites had higher nutrients contents than did species from drier sites. We also found intraspecific variations in phosphorus, potassium and magnesium contents along the water-regime gradients in the different populations of *H. splendens* (Table 1). Populations from wet habitats had higher nutrient contents than did those from drier habitats. In contrast, we observed no intraspecific variations in nitrogen and calcium contents in *H. splendens* along the water-regime gradients (Table 1).

Total carbohydrate contents in moss species from wetter sites tended to be lower than those in moss species from xeric site (Table 1). We observed clear intraspecific variations in total carbohydrate along the water-regime gradients in *H. splendens* (Table 1). Populations of *H. splendens* from hydric sites had lower total carbohydrate contents than did populations from drier sites. The contents of lignin-like compounds, extractives and carbon snowed no clear trend along the water-regime gradients.

Table 1
Organic chemical, carbon, and nutrient contents of three moss species, ranked from the most hydric to the least hydric species.

Species (water regime)	Lignin-like compound	Total carbohydrate	Extractives	Carbon	Nutrient				
					Nitrogen	Phosphorous	Potassium	Calcium	Magnesium
Calliergon giganteum (Hydric)	27.34 (0.93)*a*	50.81 (3.51)*a*	1.92 (1.22)*a*	45.89 (0.62)*a*	1.37 (0.27)*a*	0.20 (0.05)*a*	0.95 (0.12)*a*	1.43 (0.08)*a*	0.36 (0.03)*a*
Hylocomium splendens (Hydric)	26.79 (0.55)*a*	47.89 (2.68)*ab*	3.74 (0.96)*b*	43.43 (1.56)*b*	0.87 (0.09)*b*	0.11 (0.01)*b*	0.49 (0.12)*b*	0.71 (0.09)*b*	0.25 (0.04)*b*
Hylocomium splendens (Mesic)	29.93 (1.78)*b*	51.84 (1.70)*ac*	4.86 (1.54)*bc*	47.44 (0.93)*c*	0.84 (0.06)*b*	0.10 (0.01)*b*	0.37 (0.04)*c*	0.56 (0.19)*b*	0.16 (0.05)*c*
Hylocomium splendens (Xeric)	27.86 (0.76)*a*	57.40 (3.31)*d*	4.65 (0.77)*bc*	46.67 (0.61)*ac*	0.88 (0.08)*b*	0.08 (0.02)*c*	0.30 (0.02)*c*	0.67 (0.07)*bc*	0.13 (0.02)*c*
Racomitrium lanuginosum (Xeric)	17.28 (1.36)*c*	66.83 (1.47)*e*	3.08 (0.49)*ab*	41.65 (0.87)*d*	0.35 (0.05)*c*	0.03 (0.00)*d*	0.10 (0.01)*d*	0.36 (0.13)*c*	0.07 (0.01)*d*

Values (in % dry weight) are the mean of six replicates (except for four replicates in *R. lanugisnosum*). Figures in parentheses are standard deviations. Italicized letters designate significantly different values within each column ($P < 0.05$, ANOVA, Fisher's PLSD test).

Table 2
C:N, C:P and N:P ratios of three moss species and populations, ranked from the most hydric to the least hydric species.

Species (water regime)	C:N ratio	C:P ratio	N:P ratio
C. giganteum (Hydric)	35 (7)*a*	247 (59)*a*	7.1 (0.8)*a*
H. splendens (Hydric)	50 (6)*b*	387 (44)*b*	7.8 (0.8)*a*
H. splendens (Mesic)	57 (4)*b*	463 (68)*b*	8.2 (1.0)*a*
H. splendens (Xeric)	54 (5)*b*	577 (124)*c*	10.8 (2.2)*b*
R. lanuginosum (Xeric)	121 (14)*c*	1247 (79)*d*	10.3 (0.7)*b*

Values (based on dry weight) are the mean of six replicates (except for four replicates in *R. lanugisnosum*). Figures in parentheses are standard deviations. Italicized letters designate significantly different values within each column ($P < 0.05$, ANOVA, Fisher's PLSD test).

To identify further trends of nutrient status, we analyzed the stoichiometry of C:N:P ratios (Table 2). We found clear interspecific variations in C:N and C:P ratios along the water-regime gradients, and found intraspecific variations C:P and N:P ratios according to water regime in the different populations of *H. splendens*. Based on N:P ratio, the five target moss samples were divided into two groups: hydric/mesic and xeric water regimes.

4. Discussion

Our interspecific comparison revealed a clear correlation between the nutrient contents of mosses and water availability (Table 1). The observation of a higher nutrient content in mosses species from wet habitats is in agreement with previous results obtained from studies of Arctic and Antarctic bryophytes (Christie, 1987; Davey, 1999; Parkarinen and Vitt, 1974; Vitt and Parkarinen, 1977). However, the absence of any differences in nitrogen and calcium contents among the different populations of *H. splendens* indicates that low water availability does not always lead to low nutrient content (especially in the case of nitrogen).

C. giganteum growing in the most hydric habitat, contained a high calcium concentration (1.43%) compared to the other moss species, although Brown and Buck (1979) reported that calcium concentration in bryophytes is not related to water availability. A calcium concentration of 1.43% is similar to that found in calcicole mosses (Allen et al., 1967), which show a high cation-exchange capacity (Bates, 2000). Accordingly, our results suggest that *C. giganteum* may have an enhanced cation-exchange capacity, similar to that of calcicole mosses.

The high carbohydrate content of moss species and populations in dry habitats, as observed in the present study, is consistent with the observations of maritime Antarctic bryophytes (Davey, 1999). In the

present study, total carbohydrates included structural (cell-wall materials) and soluble carbohydrates (sugars and starch). The latter is generally found in high concentrations in the gametophytes of mosses from wet habitats (Melick and Seppelt, 1992; Parkarinen and Vitt, 1974; Robinson et al., 2000; Smirnoff, 1992). Thus, we may advocate that the increase in carbohydrate content observed with decreasing water availability reflects the augmentation of cell-wall material in the moss gametophytes. The finding of Proctor (1979) that mosses growing in xeric habitats display a marked increase in cell-wall to cell-volume ratio gives further credence to this idea. Additional studies may be required to validate these hypotheses.

In the present study, the C:N:P ratios in mosses were strongly correlated with water availability, although the relationship varied among the three ratios (Table 2). We found a clear interspecific in variation of C:N ratio along the water-regime gradients (Table 2), consistent with the results of previous studies on Arctic mosses (Parkarinen and Vitt, 1974), although contrary to the results of Davey's (1999) study of Antarctic mosses. In addition, we found no variation in C:N ratio within the different populations of *H. splendens* along the water-regime gradients (Table 2). This finding suggests that the C:N ratio depends mainly on interspecific variation. In contrast, we found both inter- and intraspecific variations in C:P ratio along the water-regime gradients (Table 2). The C:P ratio in *R. lanuginosum* was much higher than that in other species. For the C:P ratio, interspecific differences are possibly more important than water-regime differences.

The N:P ratio enabled differentiation between mosses growing in hydric and xeric site (Table 2). The higher C:P and N:P ratios obtained in xeric site suggest that low water availability may render mosses phosphorus-limited. The stoichiometry of N:P ratio in plant tissues is commonly used as an indicator of nutrient limitation or growth strategy (Ågren, 2004; Britton and Fisher, 2007; Güsewell, 2004; Tessier and Raynal, 2003). The N:P ratio of mosses has potential as an indicator of ecophysiological characteristics related to water availability. Further studies may be required to fully understand this relationship.

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